

A review of the copepod endoparasites of brittle stars (Ophiuroida)

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Summary

A new family, the Chordeumiidae, is proposed for six genera of copepods that live as endoparasites of brittle stars. The status of these genera, *Chordeumium*, *Arthrochordeumium*, *Lernaeosaccus*, *Ophioicodes*, *Ophioika* and *Parachordeumium* is reviewed. The genera *Ophioithys* and *Amphiurophilus* are recognised as subjective synonyms of *Parachordeumium*. The sole species of *Lernaeosaccus* is reinterpreted and redescribed. Examination of the holotype of *L. ophiacanthae* revealed that it was originally described upside down. *Codoba discoveryi* is also redescribed from the types but cannot be placed in any of the existing families of the Siphonostomatoida at present.

Introduction

In his review of copepods associated with invertebrate hosts Gotto (1979) listed eight genera of endoparasites that utilise brittle stars as hosts. None of these has formally been placed in a family and even their ordinal placement is uncertain. There are obvious taxonomic problems concerning these genera which need to be resolved before their phylogenetic relationships with other copepods can be understood. Most of the species contained in these 8 genera have highly transformed females with bizarre body morphology in the adult and few, if any, recognisable limbs. However, in some genera either males or developmental stages are known and these provide more taxonomically useful information. The monotypic genus *Codoba* Heegaard is much less modified, still retaining a more-or-less cyclopiform facies in the adult female (Heegaard, 1951). *Codoba* is redescribed, based on the type material, and the taxonomic status and phylogenetic relationships of the other genera endoparasitic in ophiuroids are reassessed. The morphology of the monotypic genus *Lernaeosaccus* Heegaard is reinterpreted and a new description and diagnosis of the genus is provided.

Descriptions

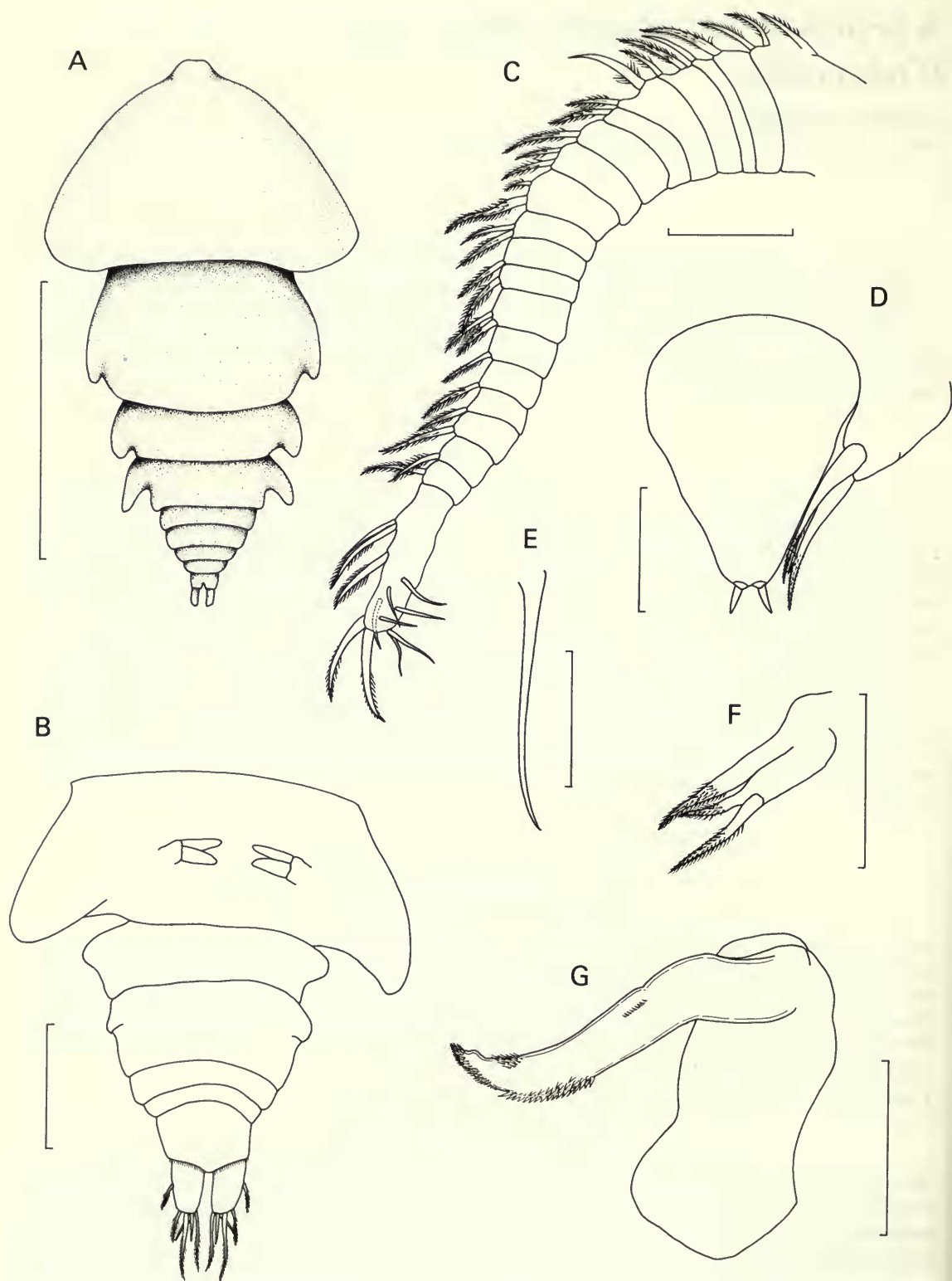
Genus *CODOBA* Heegaard, 1951

DIAGNOSIS. Adult female prosome 4-segmented, slightly swollen; urosome 5-segmented. Caudal rami distinct, bearing 6 setae. Antennule 20-segmented, lacking aesthetascs. Antenna reduced to unarmed process. Mouth tube well developed. Mandible stylet-like, without teeth; palp absent. Maxillule bilobed, inner lobe with 1, outer with 2 setae. Maxilla with distal recurved claw. Maxilliped 3-segmented. Legs 1–4 biramous, rami medially directed, intercoxal sclerites absent. Leg 5 lacking. Male unknown.

TYPE SPECIES. *Codoba discoveryi* Heegaard, 1951 by monotypy.

Codoba discoveryi Heegaard, 1951

ADULT FEMALE. Body (Fig. 1A) slightly transformed cyclopiform, but with distinct segmentation. Prosome swollen, comprising cephalothorax incorporating first pedigerous somite, and 3 free pedigerous somites. Total body length of figured syntype 1.97 mm. Each free pedigerous somite with a pair of posterolaterally directed epimeral processes. Urosome short (Fig. 1B), comprising



somite of leg 5 ($95 \times 398 \mu\text{m}$), the genital complex ($130 \times 130 \mu\text{m}$), 2 postgenital somites ($40 \times 235 \mu\text{m}$, $25 \times 190 \mu\text{m}$) and the anal somite ($115 \times 150 \mu\text{m}$). Genital apertures unarmed; located ventrolaterally on genital complex. Anal somite with row of spinules along posterior margin. Caudal rami (Fig. 1B) about 1.5 times longer than wide ($80 \times 53 \mu\text{m}$); armed with a lateral seta about at midlength, a naked dorsal seta and 4 distal margin setae, 3 of which are pinnate.

Antennule (Fig. 1C) 20-segmented; lengths of segments measured along posterior margin 13, 9, 5, 10, 11, 10, 13, 12, 12, 9, 9, 9, 18, 15, 14, 11, 15, 14, 11 and $61 \mu\text{m}$; armature elements as follows: I—3, II—1, III—1, IV—2, V—2, VI—1, VII—1, VIII—2, IX—2, X—2, XI—1, XII—1, XIII—2, XIV—1, XV—1, XVI—1, XVII—1, XVIII—1, XIX—1, XX—12. No aesthetascs present. The size and number of armature elements on the apical segment indicate that it is derived by fusion of 2 or more segments. Antenna vestigial; reduced to small unarmed process located between base of antennule and mouth tube (Fig. 2F).

Mouth tube (Fig. 1D) well developed, formed from labrum and labium. Mandible (Fig. 1E) stylet-like, unarmed; palp lacking. Maxillule bilobed (Fig. 1F); inner lobe represented by single hirsute seta; outer lobe short, armed with 2 hirsute setae. Maxilla (Fig. 1G) comprising unarmed syncoxa and distal basis. Basis drawn out into recurved claw, armed distally with patches of denticles as figured. Maxilliped (Fig. 2A) 3-segmented; basal segment armed with a row of spinules; second segment elongate, armed with a single seta and several rows of spinules; third segment bearing a tiny seta proximally on outer margin, a small inner seta and 2 unequal apical spines. Spines dentate, $51 \mu\text{m}$ and $41 \mu\text{m}$ in length. Fine spinules present around apex.

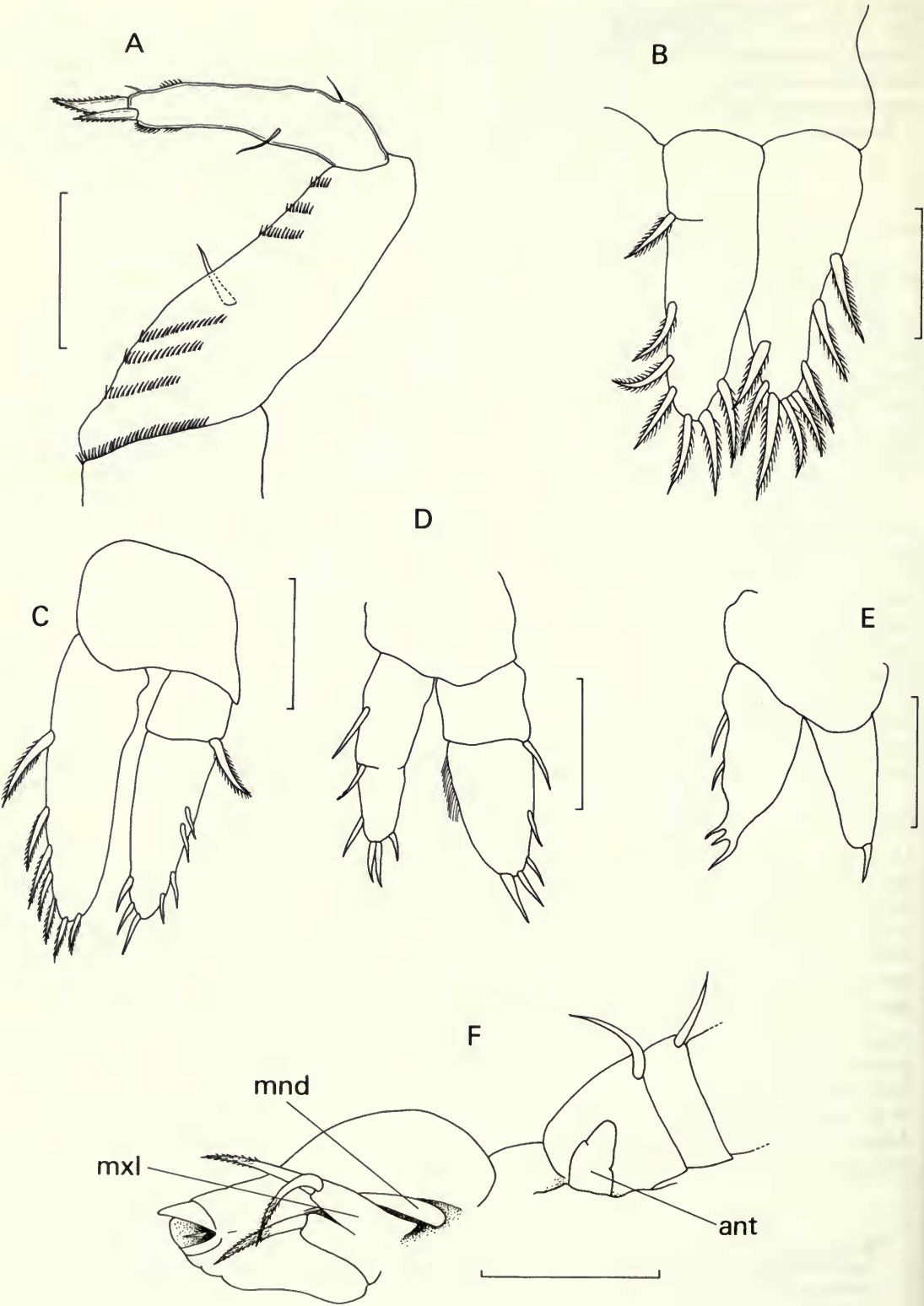
Swimming legs 1 to 4 biramous, positioned on ventral surface of somite with rami directed medially (Fig. 1B); intercoxal bars (sclerites) absent. Leg 1 (Fig. 2B) with unarmed protopod; exopod unsegmented, bearing 4 pinnate setae along outer margin, 2 at apex and 2 distally on inner margin; endopod indistinctly 2-segmented, bearing 4 pinnate setae along inner margin, 2 at apex and 1 distally on outer margin. Leg 2 (Fig. 2C) with unarmed protopod. Exopod 2-segmented; first segment with outer pinnate seta, second with 4 naked setae on outer margin, 1 at apex and 2 on inner margin. Endopod unsegmented; with 5 pinnate setae along inner margin and 2 at apex. Leg 3 (Fig. 2D) with unarmed protopod; both rami indistinctly 2-segmented. Exopod with outer seta on first segment, second with 2 outer and 2 apical setae, and a row of spinules medially; endopod with 2 inner margin setae on first segment; second with 1 inner, 1 outer and 2 apical setae. Leg 4 (Fig. 2E) with unarmed protopod; exopod with single apical seta; endopod with 2 setae on inner margin and 3-branched spinous projection apically. Leg 5 lacking.

Egg sacs lacking, eggs loose inside capsule with adult female. Capsule of specimen 1987.244 containing 44 eggs; eggs large, lecithotrophic, diameter approximately $190 \mu\text{m}$.

MATERIAL EXAMINED. Syntypes: Dissected syntype (BM(NH) No. 1987.243) collected from *Ophiura meridionalis* (Lyman) at *Discovery* Stn 123, in 230–250 m off South Georgia, 15.12.1926. Intact syntype (BM(NH) No. 1987.244) from *O. meridionalis* at *Discovery* Stn 156, in 236 m off South Georgia, 20.1.1927. Third syntype an empty capsule (BM(NH) No. 1987.245) collected from *Amphiura belgicae* Koehler at *Discovery* Stn 160, in 177 m off South Georgia, 7.2.1927. These are the data on the labels with the specimens and do not correspond in some details with those data published by Heegaard (1951).

REMARKS. When Heegaard (1951) erected the genus *Codoba* he indicated that new families would probably have to be established to accommodate the copepods parasitic on echinoderms but felt that it would be premature to do so in view of the lack of knowledge of the group. The high number of antennular segments in *Codoba* is a plesiomorphic character and is typical of the family Asterocheridae but the genus cannot be referred to the Asterocheridae as it lacks a mandibular palp and an aesthetasc on either the penultimate or antepenultimate segment of the antennule.

Fig. 1 *Codoba discoveryi* Heegaard, 1951. Adult female syntype. A, dorsal; B, Fourth pedigerous somite and urosome, ventral; C, Antennule, ventral; D, mouth cone and maxillule, anteroventral; E, Mandible, anterior; F, Maxillule, lateral; G, Maxilla, posterior. Scale bars $100 \mu\text{m}$ unless otherwise stated: A = 1 mm , B = $200 \mu\text{m}$, c = $50 \mu\text{m}$.



These are regarded as diagnostic characters for the Asterocheridae by Stock (1987). The very reduced antenna is rare in siphonostomatoids, occurring mainly in species of the Nicothoidae. However, *Codoba* is not related to the Nicothoidae which primitively have reduced antennules and a well developed antenna. The typical subchelate antenna of siphonostomatoids is primarily an organ for grasping the host and its reduction is here interpreted as an adaptation to endoparasitism. Subject to a full review of the families of siphonostomes parasitic on invertebrates, which is in progress, the genus *Codoba* is left unassigned to any of the families recognised at present.

Review of other endoparasitic genera and species

AMPHIUROPHILUS Delamare Deboutteville, 1962

In his revision of the members of the family Philichthyidae parasitic on European fishes Delamare Deboutteville (1962) correctly removed *Philichthys amphiuroides* Hérourard, 1906 from the genus *Philichthys* Steenstrup, 1862 on the basis of differences in male morphology. He established a new genus, *Amphiurophilus*, to accommodate *Philichthys amphiuroides*. *Amphiurophilus* is a junior objective synonym of *Ophiothys* which was established by Heegaard in 1951 with the same type species, *Philichthys amphiuroides* of Hérourard (1906). It is a subjective synonym of *Parachordeumium* Le Calvez, 1938 (see below).

ARTHROCHORDEUMIUM Stephensen, 1918

DIAGNOSIS. Postmetamorphosis adult female highly transformed; body somewhat dorsoventrally compressed, indistinctly segmented and with short, paired lateral processes. Two pairs of limbs present; antennules and maxillae. Antennules unsegmented, bifid at tip. Maxillae 3-segmented, including terminal claw. Egg masses irregularly wrapped around body.

Male and copepodid unknown.

TYPE SPECIES. *Arthrochordeumium appendiculosum* Stephensen, 1918 (by subsequent designation, Stephensen, 1933).

This is a valid genus established by Stephensen (1918) for *A. appendiculosum*. A second species, *Arthrochordeumium asteromorphae*, was described by Stephensen (1933).

CHORDEUMIUM Stephensen, 1918

DIAGNOSIS. Postmetamorphosis adult female moderately transformed; body cylindrical with paired lateral swellings on genital complex only; segmentation distinct. Median process present posterodorsally on genital complex. Three pairs of cephalic appendages present. Antennules unsegmented, bifid at tip. Antennae reduced to papilliform processes. Maxillae 3-segmented, including terminal claw. Legs 1 to 4 represented by slender, laterally-directed processes. Egg mass extruded posteriorly into cyst surrounding parasite.

Adult male similar to female in general facies but with better defined segments. Posterodorsal median process absent. Testes paired.

Copepodid stage without discrete caudal rami, caudal setae located on margin of anal somite.

TYPE SPECIES. *Chordeumium obesum* (Jungersen, 1912).

This genus was proposed by Stephensen (1918) as a replacement name for *Chordeuma* of Jungersen (1912). *Chordeuma* was preoccupied for a genus of Myriapoda (Kock, 1847). The type species, *Chordeuma obesum*, described by Jungersen (1912, 1914) becomes the type species of *Chordeumium* by monotypy.

Fig. 2 *Codoba discoveryi* Heegaard, 1951. Adult female syntype. A, Maxilliped, posterior; B, Leg 1, ventral; C, leg 2, ventral; D, leg 3, ventral; E, leg 4, ventral; F. Area between mouth cone and antennule showing antenna (ant), mandible (mnd) and maxillule (mxl). All scale bars 100 μ m.

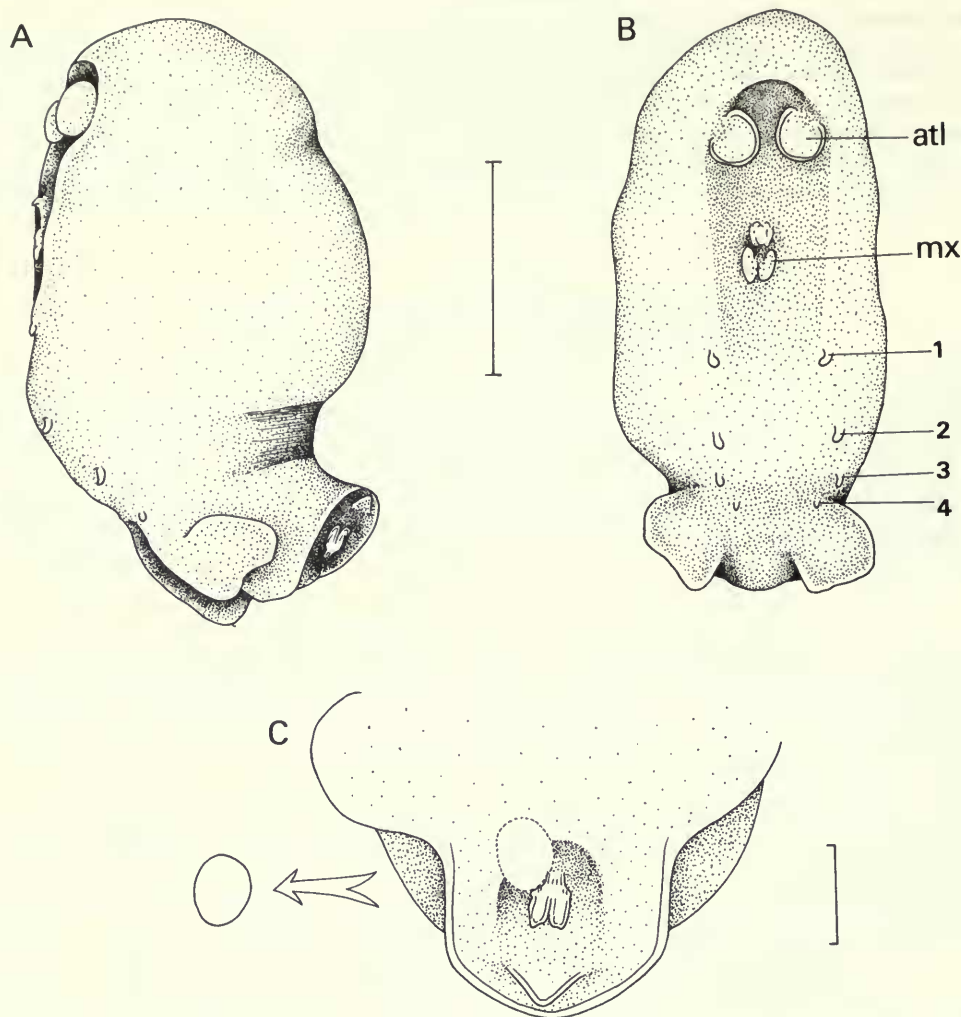


Fig. 3 *Lernaeosaccus ophiacanthae* Heegaard, 1951. Holotype female. A, lateral; B, ventral view showing antennules (atl), presumed maxillae (mx) and legs 1-4 (1-4); C, Posterior end of body, posterodorsal view showing median abdominal process and position of detached egg. Scale bars 1 mm unless otherwise stated: c = 0.25 mm.

LERNAEOSACCUS Heegaard, 1951

DIAGNOSIS. Postmetamorphosis adult female sac-like, lacking external segmentation. Single pair of lateral processes present on trunk. Posterior end concave containing a median posterior lobe. Lobate antennules and vestigial maxillae present anteriorly. Swimming legs 1-4 reduced to tiny, posteriorly directed lobes. Eggs large, released into masses surrounding female.

Male and copepodid stages unknown.

TYPE SPECIES. *Lernaeosaccus ophiacanthae* Heegaard, 1951 (by monotypy).

Lernaeosaccus ophiacanthae Heegaard, 1951

POSTMETAMORPHOSIS FEMALE. Body (Fig. 3A) highly transformed, lacking distinct segmentation

and tagmosis. Body swollen, rounded anteriorly and dorsally, flattened ventrally and concave posteriorly. Total body length of holotype 2.87 mm. Posterior part of body of holotype reflexed dorsally, probably due to fixation. Single pair of lateral lobes present posteriorly behind fourth legs (Figs 3A–B). Concave posterior end containing genital openings, a median abdominal process and a median lobe. The median abdominal process originates close to the genital apertures (Fig. 3C). Eggs located at genital openings removed during examination. Eggs large; maximum diameter 173 μ m. Egg masses not contained within sacs; wrapped around body within capsule produced by host.

Antennules represented by unarmed lobes (Fig. 3B, atl). Oral area obscured on holotype but apparently comprising a median structure and a pair of more posteriorly located limbs (probably maxillae, Fig. 3B, mx). Legs 1–4 present, reduced to unsegmented, unarmed and posteriorly directed lobes on ventral body surface (Fig. 3B, 1–4).

MATERIAL EXAMINED. Holotype: Adult female (BM(NH) No. 1982.242) collected from *Ophiacantha disjuncta* (Koehler) at Discovery Stn 190, in 316 m off the Palmer Archipelago on 24.03.1926. The depth and date on the label differ from those given by Heegaard (1951), which were 278 m and 14.03.1926 respectively.

REMARKS. This species was described by Heegaard (1951) upside down. The paired structures referred to by Heegaard as maxilliped 2 (Heegaard, 1951: Fig. 4b) are eggs. Dissected from the holotype, they were found to contain a nauplius at an early stage of development but with 3 recognisable pairs of appendages. The structure identified as a mouth cone containing mandibles is here reinterpreted as a median abdominal lobe. The thickening of the cuticle was misinterpreted by Heegaard as the paired mandibles. Close inspection of the trunk of the holotype revealed 4 pairs of posteriorly directed legs that were overlooked by Heegaard (1951). This parasite is closely related to *Chordeumium obesum*. The body morphology and appendage positioning are very similar. They are maintained as separate genera because of the differences in structure of the posterior part of the body.

***OPHIOICODES* Heegaard, 1951**

DIAGNOSIS. Postmetamorphosis adult female highly transformed; body asymmetrical, irregularly shaped and provided with numerous lateral and dorsal processes. No traces of segmentation visible. Female with midventral groove.

Male highly transformed; body elongate, unsegmented and with a pair of long, slender lateral processes. Testes paired. Male lies in midventral groove of female.

Copepodid stage unknown.

TYPE SPECIES. *Ophioicodes asymmetrica* (Pyefinch, 1940).

This is a valid genus. It was established by Heegaard (1951) on the basis of differences in male morphology between *Ophioica asymmetrica* Pyefinch, 1940 and the other 3 species of *Ophioica* Stephensen, 1933. He designated *Ophioica asymmetrica* Pyefinch, 1940 as type.

***OPHIOIKA* Stephensen, 1933**

DIAGNOSIS. Postmetamorphosis adult female highly transformed. Body unsegmented, apparently globular due to positioning of about 5 pairs of long lateral processes which curve ventrally. Four to six egg masses held within space enclosed by processes. Pair of small anterior processes possibly representing antennules. No other limbs recognisable. Median conical process may represent oral cone.

Males degenerate body form with single well developed testis, male penetrating body of female. Copepodid unknown.

TYPE SPECIES. *Ophioika ophiacanthae* Stephensen, 1933.

This genus was established by Stephensen (1933) to accommodate *Ophioika ophiacanthae*

Stephensen 1933. This becomes the type species by monotypy. Stephensen (1935) added a second species, *Ophioica appendiculata*, misspelling the generic name *Ophioika*. This is corrected here.

OTHER SPECIES. *Ophioikia appendiculata* Stephensen, 1935; *Ophioika tenuibranchia* Heegaard, 1951.

OPHIOITHYS Heegaard, 1951

Heegaard (1951) recognised the close relationship between *Philichthys amphiuræ* and the genus *Ophioika*. He removed this species from *Philichthys* and proposed a new genus, *Ophioithys*, with *P. amphiuræ* Hérouard, 1906 as type. This name is a senior objective synonym of *Amphiurophilus* as both genera have the same designated type species. This genus is, however, recognised herein as a synonym of *Parachordeumium* Le Calvez, 1938 (see below).

PARACHORDEUMIUM Le Calvez, 1938

DIAGNOSIS. Postmetamorphosis female highly transformed; body symmetrical, unsegmented, lacking limbs except for maxillae. Body with 4 pairs of major lateral processes, sometimes branched, forming enclosure containing egg masses; several paired and/or median papillae present dorsally; abdominal process well developed. Genital apertures paired. Maxillae 3-segmented, including terminal claw.

Adult male small, highly transformed, living in permanent association with female; body unsegmented, drawn out into long abdominal process posteriorly, anteriorly with pair of long lateral processes. Maxillae 3-segmented, including terminal claw.

Copepodid hatching with 3-pairs of developed biramous legs; lacking discrete caudal rami, caudal setae located on margin of anal somite. Antennules 5-segmented. Antenna 3-segmented, lacking exopod. Maxillae 3-segmented with terminal claw. Other cephalic appendages absent.

This is a valid genus established to accommodate a single species, *P. tetraceros* Le Calvez 1938, which was the type species by monotypy. The dorsal and ventral figures of the adult postmetamorphosis female *P. tetraceros* given by Le Calvez (1938) do not differ significantly from the figures in the detailed redescription of *Amphiurophilus amphiuræ* by Goudey-Perrière (1979). Both these species inhabit the genital bursae of the *Amphipholis squamata* Della Chiaje in European waters and it is here proposed that they be synonymised. The oldest available name for this species is *Parachordeumium amphiuræ* (Hérouard, 1906) and this is the type species of *Parachordeumium*.

TYPE SPECIES. *Parachordeumium amphiuræ* (Hérouard, 1906) new combination. (syn. *P. tetraceros* Le Calvez, 1938).

The three new species described by Goudey-Perrière (1979) and placed within the genus *Amphiurophilus* are here transferred to the genus *Parachordeumium*. These new combinations are: *Parachordeumium bocqueti* (Goudey-Perrière, 1979); *Parachordeumium humesi* (Goudey-Perrière, 1979); *Parachordeumium hendleri* (Goudey-Perrière, 1979).

REMARKS. The third appendage of the copepodid stage of *P. amphiuræ* (as *Amphiurophilus amphiuræ* was identified as the mandible by Goudey-Perrière (1979). This limb is retained in the adult of both sexes. Its morphology (the segmentation and possession of a terminal claw) is most atypical for a mandible and this limb is here reinterpreted as the maxilla.

CHORDEUMIIDAE New Family

DIAGNOSIS. Copepods endoparasitic in ophiuroids; adult females more-or-less highly transformed typically losing external segmentation and often with paired lateral and median dorsal or posterior processes. Lateral processes where fully developed forming 'cage' enclosing egg masses. Cephalic appendages reduced or absent; antennules and maxillae typically retained in adult. Antenna sometimes present as vestige in adult. Maxillipeds absent. Legs 1-4 reduced to uniramous processes or absent. Eggs or egg masses retained within cyst of host origin enclosing female. Adult male typically transformed, with at most one pair of lateral processes. Maxillae typically retained

by adult male, sometimes antennules and antennae also. Copepodid larva lacking discrete caudal rami; caudal setae present on margin of anal somite.

TYPE GENUS. *Chordeumium* Stephensen, 1918.

OTHER INCLUDED GENERA. *Arthrochordeumium*, *Lernaeosaccus*, *Ophioicodes*, *Ophioika* and *Parachordeumium*.

Discussion

It is difficult to produce a meaningful diagnosis for the new family because so many of the species are extremely modified for their endoparasitic mode of life. Comparison between the better known species, *Chordeumium obesum* and *Parachordeumium amphiurae*, provides the best apomorphy for the family, based on the developmental stages. Both *C. obesum* and *P. amphiurae* lack discrete caudal rami in the copepodid stage (Jungersen, 1914; Goudy-Perrière, 1979). This character is rare in copepods and serves to link *Chordeumium* and *Parachordeumium*. This relationship is central to the definition of the family because the former genus shares several characters (the structure of the antennules and maxillae in the adult female, for example) with *Arthrochordeumium* and the latter, several characters of gross female morphology (the possession of paired lateral processes enclosing the egg masses, for example) with the genera *Ophioicodes* and *Ophioika*. The genus *Lernaeosaccus*, now reinterpreted, is apparently closely related to *Chordeumium*. Both genera have retained legs 1–4 as tiny lobes in the adult female, both have a pair of lateral processes posteriorly and both have a median abdominal process located just posterior to the gonopores.

The new family is placed in the order Siphonostomatoida on the basis of the reports of a mouth cone in *Ophioika* by Stephensen (1935). The mouth cone described by Heegaard (1951) in *Lernaeosaccus* is an abdominal process. It is probable that the highly modified female body from has been derived independently within the family, from a siphonostomatoid precursor that moved freely over the surface of the brittle stars. The species of the family Cancerillidae are typically ectoparasites of brittle stars (Emson *et al.*, 1985) and the family Asterocheridae contains species that live in the stomach of basket stars (Humes, 1986). A common ancestor shared with either of these families could have made the step towards a specialised endoparasitic existence. A relationship with the highly transformed families of fish parasites, such as the Chondracanthidae, Lernaeopodidae and Philichthyidae, is regarded as extremely improbable.

The endoparasitic *Cucumaricola notabilis* Paterson, 1958 may be closely related to the Chordeumiidae. The highly transformed morphology of the adult female, with its paired lateral processes, resembles that of the chordeumiids. Also, this species retains only the antennules, antennae and maxillae in the adult female (Paterson, 1958), as in *Chordeumium* itself. It differs from the new family in having discrete caudal rami in the copepodid stage, although the presence of 5-segmented antennules at this stage is another similarity between *Cucumaricola* and *Parachordeumium*.

Acknowledgement

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